GROWTH AND POLYMORPHISM IN THE LARVA OF THE ARMY ANT (ECITON (E.) HAMATUM FABRICIUS)[1, 2]

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The army ant *Eciton* (*E.*) *hamatum* has been one of two species in the genus subjected to systematic investigation by Schneirla (1933, 1938, 1949a, 1949b). These investigations, directed primarily at behavioral analysis, have brought to light the significance of the unique broods and of events centering around brood development in these interesting ants. Although the adult worker of this species was described by Fabricius in 1781 and by Latreille in 1802, the developmental biology of the brood has escaped specialized attention in the literature except for a preliminary report by G. C. Wheeler (1943) on the external morphology of the worker larva. The present study was undertaken to investigate systematically the characteristics of development in the larval stages of this species.

Eciton hamatum exhibits the not uncommon phenomenon among ants of polymorphism in the adult worker series. That is, in this species the worker population ranges from the smallest worker minor to the large soldier form. The most general characteristic of this population series is overall size, and further quantitative differentiation through the series is found in characteristics such as mandibular and head patterns. Although in detail the series exhibits a considerable amount of quantitative

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variation, there is a smooth series or regular transition in body length from the smallest to the largest form. In order to find what differences in the larval stages of development might forecast adult polymorphism, it was essential to examine closely the condition of all types of individuals in the brood at various representative stages of development.

To appreciate the specialized nature of the problems confronting this investigation, it is imperative to bear in mind the rather unique nature of a "brood" in *E. hamatum* and other species of *Eciton* (*Eciton*). After descriptions by Schneirla (1933, 1938, 1944) an Eciton worker brood may be defined as an immense series of individuals developing more or less in step from eggs laid within the same period of a few days. Schneirla's studies have revealed a regular pattern of behavior with the colony alternating between a nomadic phase and a statary phase. The army ant queen lays a new batch of eggs within the space of several days beginning about one-third through each statary phase. Thus the ages of all individuals in one generation vary by only a few days. In *E. hamatum,* immense broods of twenty-five thousand or more eggs appear approximately every thirty-six days through the season. Most of the larval development is accomplished during the nomadic phase which commonly lasts sixteen or seventeen days in this species. At the end of the nomadic phase the larvae enclose and the colony enters the statary phase. With such material all possibility of confusing individuals of different generations is eliminated, hence Eciton appears to be an ideal form for investigations of larval development and larval polymorphism. The dorylines are the only social insects with broods of this description.

As would be expected, classification of the larvae taken from such broods at different times of development represents a formidable problem. The literature offers no convenient or satisfactory scheme for separating the larva into instars such as those which have been worked out for other holometabolous insects. G. C. Wheeler (1938) with relatively limited material, designated army-ant larvae as "young (?) or immature and as mature," with body length used as the index of maturity. However, as a single criterion body length is an uncertain and misleading characteristic in the larvae of these ants, for actually, as it proves, a difference in body length between two randomly selected larvae can be due to a difference in polymorphic status, in developmental stage (i.e., age), or in both of these. For example, when larvae are preserved from the same brood at different stages, a major-type larva arrested at an early stage of development may have the same body length as a minor-type larva arrested at a later stage of development (see Plate III, fig. 9, and Plate IV, fig. 10). Only when the developmental stage is known can the significance of body length be evaluated correctly in Eciton larvae.

The problem required working out a reliable means of allocating single larval specimens or small samples of larvae from broods of unknown status to their respective growth stages. The problem thus stated would be insoluble if body length were relied upon as our exclusive criterion, for in body length the larvae presents a smooth series or regular transition from the smallest to the largest forms, as does the adult population. However, to anticipate, in our examination of external morphology in a series of large brood samples of known status, detailed structural differences have emerged which prove diagnostic for developmental stages. The size and developmental range of these samples have made possible a scheme for classifying Eciton larvae as to developmental stage. These studies of the external morphology paved the way for a differential study of the internal changes, to be reported in a further paper.

MATERIAL AND METHODS

The observations in this paper were obtained chiefly from Bouin-fixed larvae of the colony H-1, 1947, collected on Barro Colorado Island, Canal Zone, during November 1947 (Schneirla and Brown, 1950). Specimens from other colonies HB, 1946 Schneirla, 1949a) and H-11, 1948 (Schneirla and Brown, 1950) were also studied for purposes of comparison.

The material collected in the field represents samples taken from a particular brood of a colony at regular intervals from early larval development to larval maturity. An attempt was made to get representative samples, i.e., to include all the polymorphic forms, and care was exercised to limit the size of successive samples so as not to interfere with the general brood condition. The successive samples were collected from colony H-1, between November 7 to November 21, during one of its nomadic phases. The first sample was collected an estimated three days after the onset of nomadism. This sample contained more than 300 specimens consisting of eggs and newly hatched larvae. The second sample was collected two days after the first, i.e., on the fifth nomadic day, and contained about 70 larvae. The third sample was collected on the seventh nomadic day, two days after the second sample had been collected. This sample contained between 200 and 300 larvae. Similar samples were collected on the ninth, tenth, twelfth, fourteenth, sixteenth and seventeenth nomadic days and each sample contained between 200 and 300 larvae. The samples collected on the seventeenth nomadic day contained large and intermediate larvae that had become enclosed; the small larvae of this sample had not yet enclosed. A sample collected on November 23, two days after the seventeenth nomadic day, contained only enclosed larvae. This sample was taken on the second day of the statary phase when the brood was entering the prepupal stage (Schneirla, 1949b) and is, therefore, not considered in this paper.

The imaginal leg discs, antennal discs, gonopodal discs, head capsule, and degree of pilosity were some of the external structures studied. Measurements were made on most of these structures, but since the measurements of the leg discs proved most useful in relation to the main task, our attention in this paper is confined to them. Measurements were made with an ocular micrometer.

The following method was employed for selecting larvae for the leg disc measurements. The larval sample under study for each successive day collected during the nomadic phase was emptied as a whole into a Petri dish. Then with the aid of a dissecting microscope an attempt was made to select the five smallest and the five largest larvae, as well as the five larvae closest to the intermediate size. This procedure was designed to insure observation and examination of the extremes in the size of the larvae for each sample collected for the nomadic phase. Then successive samples could be studied comparatively in terms of corresponding points, viz., comparing the characteristics of the larvae of same size at the different stages of development during the nomadic phase. Since the distribution of the small, intermediate and large forms in any one larval series of any one sample was not critical for the purposes of this investigation, a random sampling technique was not employed.

OBSERVATIONS AND RESULTS

Preliminary observations of various structures of the army ant larvae indicated that the imaginal leg discs were the most important structures for separating the larvae into stages. In *Eciton hamatum* the leg discs are found in all stages, and, more-

TABLE 1

IMAGINAL LEG DISC SIZES FOR EACH POLYMORPHIC GROUP OF LARVAE COLLECTED DURING THE NOMADIC PHASE

Nomadic Day	Larvae	Body Length in mm.	Leg Discs Length in mm.	Leg Discs Width in mm.
3rd	All Small	0.50 to 1.40	0.021 to 0.028	0.021 to 0.042
5th	Small	0.70 to 1.30	0.021 to 0.028	0.021 to 0.028
	Inter.*	2.50 to 2.90	0.042 to 0.060	0.051 to 0.084
	Large	3.60 to 4.50	0.079 to 0.084	0.098 to 0.105
7th	Small	0.90 to 1.40	0.028 to 0.028	0.028 to 0.042
	Inter.	2.30 to 3.10	0.042 to 0.060	0.051 to 0.070
	Large	3.70 to 5.50	0.098 to 0.126	0.098 to 0.112
9th	Small	4.50 to 5.20	0.103 to 0.133	0.126 to 0.135
	Inter.	6.30 to 6.50	0.147 to 0.168	0.140 to 0.145
	Large	7.60 to 8.20	0.168 to 0.173	0.145 to 0.173
10th	Small	2.90 to 4.30	0.084 to 0.107	0.084 to 0.126
	Inter.	6.60 to 7.00	0.175 to 0.217	0.163 to 0.187
	Large	8.60 to 9.50	0.241 to 0.210	0.162 to 0.201
12th	Small	3.40 to 4.10	0.084 to 0.112	0.084 to 0.126
	Inter.	6.80 to 7.50	0.226 to 0.236	0.173 to 0.196
	Large	8.40 to 9.60	0.280 to 0.280	0.210 to 0.224
14th	Small	4.40 to 4.90	0.203 to 0.217	0.149 to 0.156
	Inter.	6.60 to 7.50	0.306 to 0.352	0.217 to 0.254
	Large	9.00 to 10.0	0.420 to 0.420	0.287 to 0.280
15th	Small	4.60 to 4.80	0.226 to 0.268	0.163 to 0.175
	Inter.	8.20 to 8.70	0.446 to 0.509	0.254 to 0.320
	Large	10.0 to 10.8	0.445 to 0.515	0.273 to 0.303
16th	Small	4.10 to 5.00	0.259 to 0.287	0.182 to 0.201
	Inter.	6.50 to 7.30	0.336 to 0.420	0.227 to 0.247
	Large	8.40 to 9.20	0.351 to 0.470	0.271 to 0.305
17th	Small	4.80 to 5.50	0.327 to 0.403	0.203 to 0.210
	Inter.	Enclosed ---	--------------	--------------
	Large	Enclosed ---	--------------	--------------

* Abbreviation used in this table to indicate the intermediate larvae.

over, these are one of the few structures readily accessible to measurement, which are found to display a growth rate independent of overall size. In contrast, a statistical evaluation of our data shows that the head capsule bears a direct relationship to body length regardless of the stage of development. It is otherwise for the leg discs in relationship to body length (Text-figures 1, 2, and 3).

In very young or immature larvae the size of all three pairs of imaginal leg discs is approximately the same. The respective sizes of the leg discs, furthermore, are the same for larvae of similar body length and the same stage of development. In other words there is little, if any, individual difference in the size of the leg discs in very young larvae. In more mature larvae the three pairs of leg discs may vary slightly in size in any one specimen and may also vary to a small degree in the larvae of similar body length taken from the same stage of development. There is a greater degree of intra- and inter-individual differences in these thoracic structures in the more mature larvae. These size differences in the leg discs of the more mature larvae, however, do not mitigate the usefulness of these structures for separating the larvae into more definite stages.

Table I represents the smallest and largest body length size for each polymorphic group of larvae. The figures for the leg discs represent the average size of leg discs measured for five larvae in each of the three polymorphic groups, i.e., the polymorphic small, intermediate and large larvae. An examination of Table I indicates that larvae of the same body length but of different nomadic days have leg discs of consistently different size increasing with age (Plate III, fig. 9, and Plate IV, fig. 10). This is clearly evident if a 6.6 mm. larva of the tenth nomadic day is compared with a 6.6 mm. larva of the fourteenth nomadic day. Small larvae may be collected near the end of the nomadic phase which have larger leg discs than large larvae collected at an early stage of nomadism, clearly indicating the more advanced age of the former and their polymorphic specialization. This fact is made quite clear when the leg discs of 4.8 mm. larva of the seventeenth day is compared with those of a 9.6 mm. larva of the twelfth nomadic day. However, the most critical test comes when the size of the leg discs is compared at successive

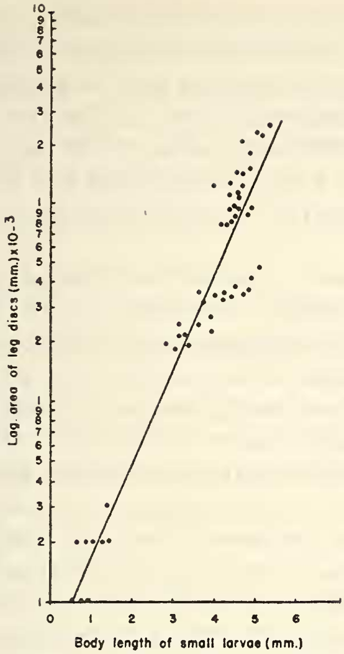

FIG. 1. Growth curve for the imaginal leg discs of polymorphic small *E. hamatum* larvae. The calculated slope is 2.864.

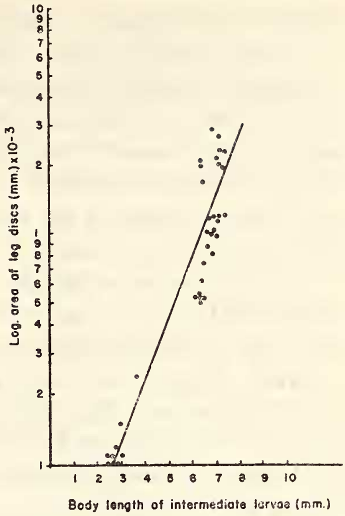

FIG. 2. Growth curve for the imaginal leg discs of the polymorphic intermediate *E. hamatum* larvae. The calculated slope is 1.785.

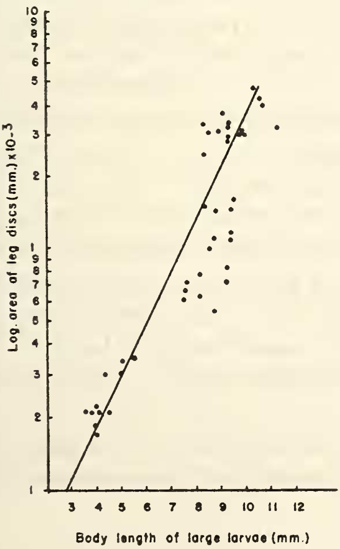

FIG. 3. Growth curve for the imaginal leg discs of the large *E. hamatum* larvae. The calculated slope is 1.635.

stages of development; for example, at the tenth, twelfth and fourteenth nomadic days. This is even a more exacting test than is the one in which earlier stages are compared since in samples taken after the tenth nomadic and especially from the fourteenth nomadic day onward, inter-stage differences in the size of the leg buds become more marked. Table I shows that despite this fact there is an increase in the leg discs in all types of larvae through the more advanced stages.

In order to get a graphic representation of the relationship which the leg discs bear to body length of the larvae, values for the area of the leg discs were plotted against the body lengths for each nomadic day for five larvae in each of the three polymorphic groups. The original data was plotted on arithmetic paper. The points plotted indicated that an exponential curve of the type $y = a\ b^x$ would best fit the relationship between body length and the area of the leg disc. In this formula y represents the area of the imaginal leg disc, x represents the body length of the larva, and a and b are constants. Each polymorphic group of larvae seems to have its own exponential curve. This was further brought out when the data was plotted on semi-logarithmic paper. A linear relationship was obtained when the leg disc area for each corresponding body length was thus plotted for the three polymorphic groups (Text-figures 1, 2, and 3). The rate of growth of the leg disc area with respect to the body length clearly varied among the three polymorphic groups of larvae, and was smallest for the large larvae, greater for the intermediate larvae, and greatest for the polymorphic small larvae. The constants a and b determine the type of exponential curve for each of the polymorphic groups. These constants were determined by the least square method. The exponential equations of the forms are for the polymorphic small larvae, $y = 0.0005801\ (2.864)^x$; for the polymorphic intermediate larvae, $y = 0.0021919\ (1.785)^x$; and for the polymorphic large larvae $y = 0.0025832\ (1.636)^x$. The larger b is, the greater is the rate of increase in the leg discs with respect to body length. The larger a is, the larger is the initial leg disc area, i.e., at the earliest stages of development.

An inspection and explanation of the figures in this paper will serve to demonstrate the most important external structures which, when correlated with leg disc size, were used for separating out the larvae into stages.

Plate I, figures 1, 2, 3, and 4, simply illustrates extremes in body length of the larvae of the third, fifth, twelfth, and fifteenth nomadic days. The extremes in body length for any one nomadic day and the overlapping of these body sizes into other days of the nomadic phase is indicative from size alone of at least three polymorphic types. The larvae collected on the third nomadic day, however, are characterized by all forms being small, transparent and anteriorly truncated. Most of the internal organs are visible through the body cuticle. The head segment in these larvae is poorly developed (Plate I, fig. 1). Plate II, figure 5, on the other hand, illustrates a typical head of a twelfth nomadic day larva which is well developed and tapering anteriorly. Sensilla turrets are clearly visible on this head segment. The head segment of the intermediate larvae of the fifth nomadic day has already assumed this shape and lost its truncated appearance. The small larvae of the fifth nomadic day possess antennal and gonopodal imaginal discs which differentiate them from any larvae of the third nomadic day.

Plate II, figure 6, illustrates another morphological character used for separating the larvae into stages, namely, the presence of a peripodal cavity which surrounds the leg discs and is present first in the large seventh nomadic day larvae.

The phenomenon of the leg discs overlapping the posterior margin of the thoracic segment in which they are found was still another character used for separating the larvae. Some of the intermediate larvae of the tenth nomadic day possess leg discs showing a precocious overlapping of these posterior margins. Only one or sometimes more than one leg disc may overlap the posterior margin of the segment. In most of the intermediate larvae of this group, however, the leg discs extend only to the posterior margin of the segment in which they are located. In the intermediate larvae of the twelfth nomadic day, the leg discs overlap the posterior margin of their segment (Plate II, fig. 7), as is the case in all larvae of succeeding nomadic days.

Segmentation of the leg discs is the last major morphological character used in separating the larvae and appears first in the intermediate fourteenth nomadic day larvae (Plate II, fig. 8).

In these specimens the leg discs appear segmented and have two or three marginal furrows which extend obliquely through the leg discs from the lateral to the median margin. The larvae of all succeeding groups also show this characteristic.

In addition to the more significant characteristics already mentioned it should be kept in mind that as the polymorphic types become mature the body width of all larvae increase in size. This is especially true for larvae collected after the fourteenth nomadic day, which have greater body widths than larvae of comparable body lengths collected prior to this period.

On the basis of larval morphological observations and data collected for leg disc sizes and body lengths, the following tentative key is proposed for separating the larvae into developmental periods based on nomadic days. It is realized that the key in its present form applies specifically to the material which was studied and variations in the measurements of the leg discs will undoubtedly occur when other *hamatum* larvae are applied. However, the measurements included are expected to be used as an aid in determining the position of the larvae with respect to the development of the other visible structures.

KEY TO THE LARVAL GROWTH STAGES OF E. HAMATUM

A. Leg discs oval or round without peripodal cavity; head segment larger than prothoracic segment .... B

B. Gonopodal discs and antennal discs absent; larvae transparent, gut and entire nerve cord visible through cuticle; body cuticle smooth C

C. Body length 0.021 mm. to 0.028 mm. in length and width .... N-3*, N-5 Small

CC. Body length approximately the same as in C but leg discs up to 0.028 mm. in length and 0.028 mm. to 0.042 mm. in width; mouth parts slightly better differentiated and sensilla turrets present .... N-7 Small

BB. Gonopodal discs and antennal discs present; larvae not transparent but first few ganglia of the ventral nerve cord visible through cuticle; body covered with irregularly arranged papillae; body lengths from 2.30 mm. to 4.50 mm., with leg disc lengths from 0.042 mm. to 0.084 mm. and widths from 0.060 mm.to 0.105 mm. .... N-5 Intermediate, N-5 Large, N-7 Intermediate

AA. Leg discs oval or round with a peripodal cavity; the prothoracic segment larger than the head segment .... B

* N-number, represents nomadic day.

B. Leg discs not overlapping the posterior margin of body segment .. C
- C. Body segments sparsely covered with short hairs and the first few ganglia of the ventral nerve cord visible through cuticle; body lengths from 3.70 mm. to 5.50 mm. with leg disc lengths from 0.084 mm. to 0.126 mm. .... N-7 Large, N-10 Small
- CC. Body segments uniformly covered with short hairs and first few ganglia of the ventral nerve cord not visible through cuticle .... D
  - D. Body lengths from 3.49 mm. to 5.50 mm. with leg disc lengths from 0.084 mm. to 0.133 mm. and widths from 0.084 mm. to 0.135 mm. .... N-9 Small, N-12 Small
  - DD. Body lengths greater than in D .... E
    - E. Body lengths from 6.30 mm. to 8.20 mm. with leg disc lengths from 0.147 mm. to 0.173 mm. and widths from 0.140 mm. to 0.173 mm. .... N-9 Intermediate, N-9 Large
    - EE. Body lengths from 6.60 mm. to 9.50 mm. with leg disc lengths from 0.175 mm. to 0.210 mm. and widths from 0.163 mm. to 0.201 mm. .... N-10 Intermediate, N-10 Large

BB. Leg discs overlapping posterior margin of body segment C
- C. Leg discs not segmented .... D
  - D. Body lengths from 4.40 mm. to 4.90 mm. with leg disc lengths from 0.203 mm. to 0.217 mm. and widths from 0.149 mm. to 0.156 mm. .... N-14 Small
  - DD. Body lengths greater than in D .... E
    - E. Body lengths from 6.80 mm. to 7.50 mm. with leg disc lengths from 0.226 mm. to 0.236 mm. and widths from 0.173 mm. to 0.196 mm. .... N-12 Intermediate
    - EE. Body lengths from 8.40 mm. to 9.60 mm. with leg disc length averaging 0.280 mm. and widths from 0.210 mm. to 0.224 mm. .... N-12 Large
- CC. Leg discs segmented .... D
  - D. Body lengths from 4.10 mm. to 5.50 mm. .... E
    - E. Leg disc lengths from 0.226 mm. to 0.268 mm. and widths from 0.163 mm. to 0.175 mm. .... N-15 Small
    - EE. Leg disc lengths and widths larger than in E ...... F
      - F. Leg disc lengths from 0.259 mm. to 0.287 mm. and widths from 0.182 mm. to 0.201 mm. .... N-16 Small
      - FF. Leg disc lengths from 0.327 mm. to 0.403 mm. and widths from 0.203 mm. to 0.210 mm. .... N-17 Small

DD. Body lengths from 6.50 mm. to 7.50 mm. .... E

E. Leg disc lengths from 0.306 mm. to 0.352 mm. and widths from 0.217 mm. to 0.254 mm. .... N-14 Intermediate

EE. Leg disc lengths from 0.336 mm. to 0.420 mm. and widths from 0.227 mm. to 0.247 mm. .... N-16 Intermediate

DDD. Body lengths from 8.20 mm. to 10.80 mm. and leg disc lengths from 0.420 mm. to 0.515 mm. and widths from 0.250 mm. to 0.305 mm. .... N-14 Large, N-15 Intermediate and Large, ... N-16 Large

DISCUSSION

In the past the study of growth processes in the larvae of social insects as the ant has been neglected by entomologists, who have turned mainly to the non-social insect for such studies. Consequently, development in social insects has not been as clearly understood as in other holometabolic insects. Reasons for this neglect are understandable. In a social organization developmental forms are confined to nests or hives, and the egg-laying of the queen is usually continuous during the warmer seasons. Hence, the larval population consists of a heterogenous mixture of individuals of mixed castes, ages and stages, often complicated by extensive worker differences in species which manifest polymorphism. Before the enigma proposed by individual differences on the adult level can be clarified, corresponding immature forms must be studied at reliably differentiated stages.

In *E. hamatum* the adult polymorphic workers form a continuous series from the smallest worker minor to the large soldier form, and appears, therefore, to involve an incomplete polymorphism. It is possible that further studies will reveal the presence of an incomplete dimorphic type of polymorphism as suggested by Wilson (1953). In the adult worker forms, as has been previously stated, beside differences in size there are apparent qualitative differences in this series marked primarily by exceptional hooked mandibles and head pattern of the major worker. However, in samples of *E. hamatum* larvae collected on successive days of the nomadic phase, characteristics such as are found in the adults to differentiate the polymorphic series, are not noticeably apparent. The obvious overlapping in the range of body sizes of the larvae for any one sample as compared with earlier or later samples collected during the nomadic phase which together with structural similarities, at first seems to defy differentiation of the larvae into growth stages. In actual fact any distinction of growth stages is impossible on the basis of body size alone. It has been further found that Dyar's rule and Prizbram's rule (Wigglesworth, 1939) are not applicable in determining the number of instars for the larvae and, therefore, the particular growth stage of the larva. Dyar's rule shows that the head capsule of caterpillars grow in a geometrical progression, increasing in width by a ratio which is constant for a given species. Prizbram's rule implies a harmonic growth where the dimensions of a part of a body increase at each moult by the same ratio as the body as a whole. Growth in all these larvae is actually disharmonic or allometric, i.e., the parts of the body grow at rates peculiar to themselves. The extremes in size in the larvae of *E. hamatum* and the over-lapping of these sizes during the different periods of the nomadic phase indicate polymorphism and is not due to instar growth.

A study of the morphological changes which accompany larval growth supports the hypothesis of polymorphism in the larvae. The norm for designating stages of larval development is based on the days of the nomadic phase as worked out by Schneirla (1938, 1949a). In terms of this norm it is possible to correlate specific characters with growth for different polymorphic larvae during the different days of the nomadic phase. However, these results show some limitations. Eggs are laid during the statary phase and embryonic development and a small amount of larval development takes place during this phase. The greatest part of larval development, however, occurs during the nomadic phase. In samples collected on the third nomadic day the most advanced members of this group were larvae measuring about 1.5 mm. in length, the least advanced members were eggs in various stages of embryonic development. Unfortunately, because of limitations in the range of our material, the earliest stages of larval development occurring prior to the nomadic phase were not available in the series used.

A visual method of selecting specimens from samples such as was employed in this study does not always insure the selection of true intermediate larvae. In some cases there is overlapping of structural characteristics of these larvae with structural characteristics of the smaller or larger forms, which would probably be indicated if polymorphism is of the incomplete dimorphic type. This difficulty might be more easily resolved if the intermediate specimens were selected at equal intervals of the size range of the sample. However, since the larvae like the adult workers apparently form a smooth series from the smallest to the largest forms, it was considered adequate to select specimens on a visual basis into categories representing the extremes and the median in body sizes. Conditions under which field samples are taken do not always permit representative samples to be obtained, hence the polymorphic extremes which make up a small percent of the population may be inadequately represented in some samples. This is the case with the measurements reported in Table I for the small larvae of the ninth nomadic day. A comparison of the ninth nomadic day larvae with those of the tenth and twelfth nomadic days indicates there must have been smaller larvae in the population than those actually obtained for the ninth nomadic day. Hence, the smallest ninth nomadic day larvae in this material shows a precocious morphological development normally present in the smallest larvae of later samples.

In appraising the present results minor visual errors must also be considered in measuring and examining small structures. The averages obtained for specimens of given size and growth stage show a consistency despite intra- and inter-individual differences in the imaginal leg disc sizes recorded for individual specimens. It is presumed that over and above the expected observer's error in measuring the leg discs for any one individual an actual growth differential exists in this respect. The nature of this growth differential is suggested in our results by a size gradient in leg disc pairs ranging from the smallest in the first pair to the largest in the third pair.

A precocious overlapping of the posterior margin of the segments by the imaginal leg discs was first observed in some of the intermediate tenth nomadic day larvae but not in the polymorphic large larvae of this group. Why this overlapping was not found in the smallest and largest larvae is not clear.

Wheeler (1938) investigated the leg vestiges in *E. hamatum* and other army ant larvae. These structures are subcircular, convex, slightly elevated cuticular papillae, which lie ventral to the imaginal discs. His figures 2, 3, and 5, show the close relationship between these vestiges and the imaginal leg discs, but the present paper is not concerned with the study of the leg vestiges. These structures were seen in many of the larvae but were not always discernible and consequently, not applicable for use as a distinguishing character.

The principle employed in this study for separating the larvae into stages and establishing the existence of polymorphism in these forms was based on the heterogonic growth of the imaginal leg discs. This principle is not a new one and has often been employed in such studies.

Investigators have observed that certain organs increase in relative size with the absolute size of the body that bears them, but Huxley (1932) was first to demonstrate the significant relationship between the magnitudes of the two variables by his heterogony formula, $y = b\ x^k$, later revised to $y = bx^a$ (Huxley and Teissier, 1936). In this revised formula, as applied to the present study, y represents leg-disc dimension, x represents body length, and b and a are growth constants, a representing the equilibrium constant and b the value of y when $x = 1$, i.e., the initial growth index. Huxley was first to show that problems in polymorphism in ants can be related to problems in allometric growth in other animals. For example, he finds that the morphological relationship of the chelae of many male and some female Decapods and other appendages of various crustacea follow the rule of constant differential growth ratios. Dudich (1923) finds that *Cyclommatus tarandus* has marked heterogenic male mandibles. Coleopterists distinguish main types based on mandible characters. Prizbram (1930) finds that the legs in Orthoptera also obey this rule. The earwig, *Forficula auricularia,* bears at the end of the abdomen a pair of cerci named ''pincers'' which vary with sex (Paulian, 1937). Measurements of the pincers show that two polymorphic types are present in the male.

In neuter social insects that show polymorphism, Huxley states that such series are characterized by relative increase of head, and especially mandible size, with an absolute increase in total size. He believes workers and soldiers represent a series of size forms of a single genetic type possessing a mechanism for heterogony or allometry of mandible and head. In ants the absolute size range appears to be greater than for other holometabolous insects, the size differences being brought about by the amount of food fed the larvae by their nurses. The largest larval forms are fed to the limit; the smallest are deprived of food and forced to pupate while still small larvae. Emery (1921) has shown this behavior to be true for ants. Wesson's work (1940) goes one step further and gives evidence that overfeeding plays an important role in the production of the large queens as against the smaller workers. More recently the studies of such invesigators as S. F. Light (1942, 1943) on the social insects, that of R. E. Gregg's (1942) on Pheidole, M. V. Brian's (1951, 1952) studies on caste determination in *Myrmica rubra,* and A. Ledoux's (1950) work in *Oecophylla longineda,* reveal evidence of caste determination during the larval stages. Flanders (1945, 1952), on the other hand, has suggested that caste determination may occur in the eggs at the period of maturation or at the time of laying. The results obtained in this investigation support caste differentiation during the larval period. Cohic (1946), making use of the rule of constant differential growth ratios, finds in the workers of *Dorylus* (*Anomma*) *nigricans* evidence for a mechanism for heterogony of the head, mandible, scape of the antenna, and leg parts and on the basis of his results separated the workers of this species into four types.

It would appear from the observations in this investigation that in the case of determination of castes in *E. hamatum,* growth trends are fixed during the larval stage and proceed without interruption to form the adult ant. The main features of adult caste formation are dependent on the differential growth of such structures as the imaginal leg discs, which possess specific growth rate potentials in the larva. The growth of the larval tissues apart from the imaginal discs is approximately regulated to allow final expression of the leg disc potentials.

On the basis of three distinct growth curves and different slopes in at least the small and large larvae good evidence is offered for believing that the size of the leg discs in relation to body length of a particular polymorphic group may provide an index of larval age, or in other terms, offer a clue to the time in the nomadic phase when a given sample was taken.

SUMMARY

A morphological study was made on several stages of worker larvae of *Eciton* (*E.*) *hamatum* to determine evidences of larval polymorphism. Specific external characters are correlated with growth and development of the larvae.

The extreme range in the body sizes permitted the separation of the larvae arbitrarily into three groups; small, intermediate and large.

The size and development of the leg discs, the shape of the head segment, the appearance of the imaginal discs, degree of transparency, and pilosity were noted for the different size larvae of each group. These characteristics are correlated with the days of the nomadic phase which have been used to designate successive stages of larval development.

The results obtained are tabulated, and a key for separating the larvae according to nomadic day is proposed. The limitations of this key have been discussed.

A comparison of the leg discs with body length indicates that these structures have an independent growth rate in the small, intermediate, and large larvae. These results are represented graphically. This independent growth rate makes possible the separation of the larvae of similar body lengths but different development stages into different polymorphic groups. It also indicates larval age.

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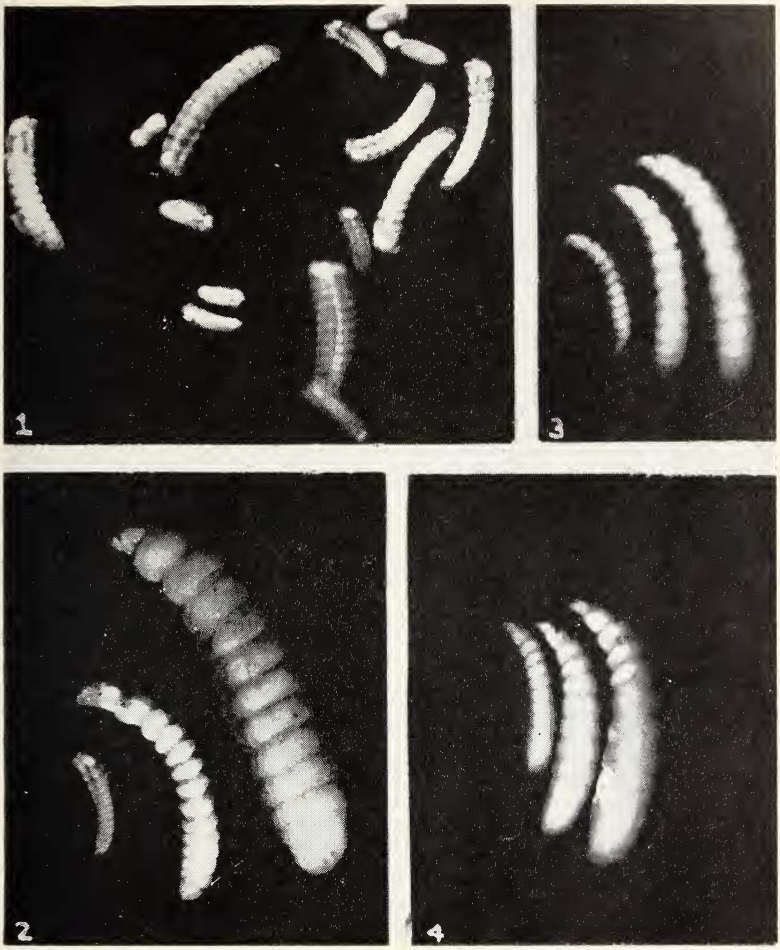


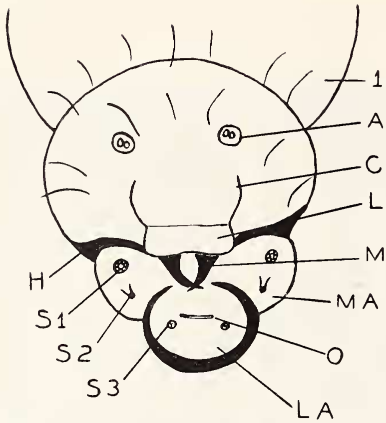
PLATE I

FIG. 1. Third nomadic day larvae of *E. hamatum*. ×19.

FIG. 2. Small, intermediate, and large fifth nomadic day *E. hamatum* larvae. ×14.

FIG. 3 Small, intermediate, and large twelfth nomadic day *E. hamatum* larvae. ×4.5.

FIG. 4. Small, intermediate, and large fifteenth nomadic day *E. hamatum* larvae. ×4.5.



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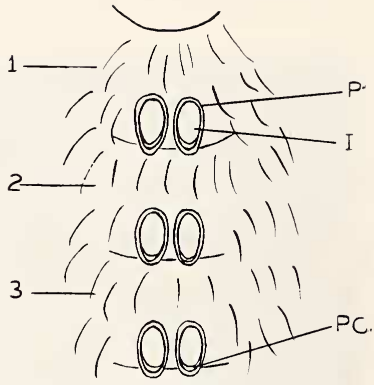

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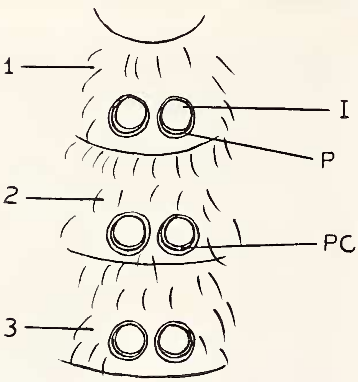

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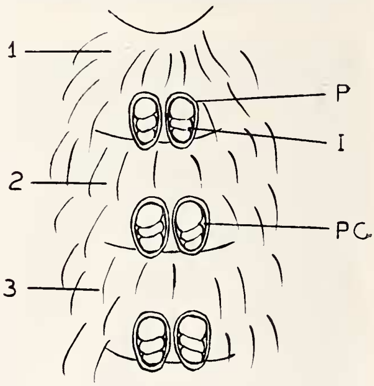

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Plate II

Fig. 5. Head of twelfth nomadic day *E. hamatum* larvae. 1, first thoracic segment; A, antennal disc; C, clypeus; H, habena maxilla; L, labrum; LA, labium; M, mandible; MA maxilla; O, opening of the spinning gland; S_1, S_2, S_3, sensilla turrets.

Fig. 6. Ventral view of the thoracic segments of a large seventh nomadic day *E. hamatum* larva. 1,2,3, first, second, and third thoracic segments; I, imaginal leg discs; P, peripodal membrane; PC, peripodal cavity.

Fig. 7. Ventral view of the thoracic segments of an intermediate twelfth nomadic day *E. hamatum* larva. 1,2,3, first second, and third thoracic segments; I, imaginal leg discs; P, peripodal membrane; PC, peripodal cavity.

Fig. 8. Ventral view of the thoracic segments of an intermediate fourteenth nomadic day *E. hamatum* larva. Labelling the same as in figures 6 and 7.

(JOUR. N. Y. ENT. SOC.), VOL. XVIII (PLATES III, IV)

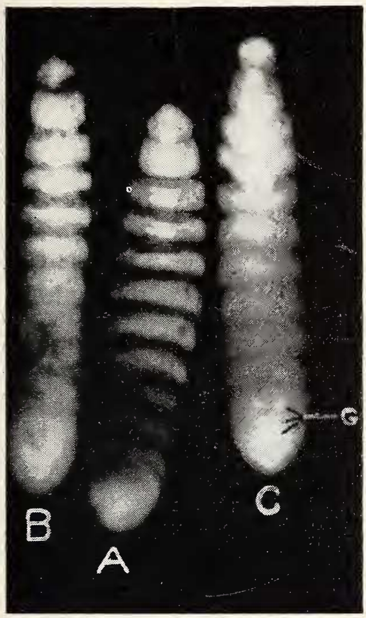

PLATE III

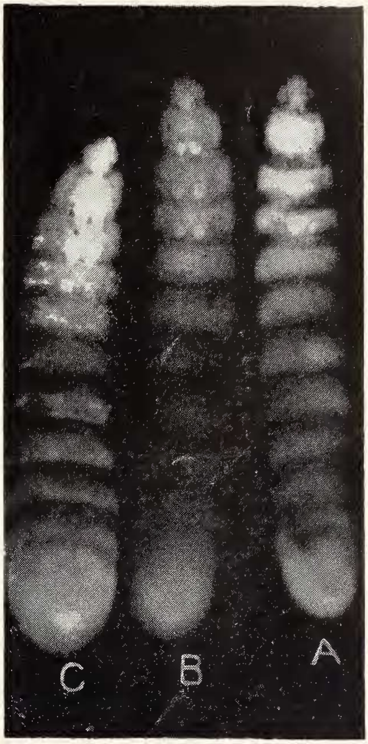

PLATE IV

PLATE III. A comparison of the size of the leg discs in 5.5 mm. *E. hamatum* larvae of different nomadic days. ×14. A, large larva of the seventh nomadic day; B, small larva of the twelfth nomadic day; C, small larva of the seventeenth nomadic day; G, gonopodal discs.

PLATE IV. A comparison of the size of the leg discs of large and intermediate *E. hamatum* larvae of different nomadic days but of nearly similar body lengths. ×14. A, large larva (8.3 mm.) of the ninth nomadic day, leg discs within the margin of the segment; B, large larva (8.5 mm.) of the twelfth nomadic day, leg discs overlap the posterior margin of the segment; C, intermediate larva (7.9 mm.) of the fifteenth nomadic day, leg discs segmented and overlap the posterior margin of the segment.